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POLLINATION OF *MIMETES HIRTUS* (PROTEACEAE) BY CAPE SUGARBIRDS AND ORANGE-BREASTED SUNBIRDS

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Abstract

Promerops cafer (Cape Sugarbird) is a major pollen vector for *Mimetes hirtus*, brushing its head and throat against pollen presenters and stigmata as it forages for nectar. *P. cafer* is attracted to partially-opened inflorescences, in particular, by virtue of the large nectar standing crops present. Maximum pollen availability and viability coincide with most visits by *P. cafer*, and result in a relatively high degree of seed set. *Nectarinia violacea* (Orange-breasted Sunbird) visits *M. hirtus* occasionally, but does not transfer significant pollen loads.

Uittreksel

BESTUIWING VAN *MIMETES HIRTUS* (PROTEACEAE) DEUR KAAPSE-SUIKERBEKKIES EN JANGROENTJIES

Promerops cafer (Kaapse-suikerbekkie), is 'n belangrike stuifmeeldraer vir *Mimetes hirtus* omdat dit met kop en keel teen die stuifmeelhokke en -stempels skuur wanneer dit nektar soek. *P. cafer* word deur die gedeeltelike oop bloeiwyses gelok, veral as gevolg van die groot hoeveelhede nektar beskikbaar. Maksimum stuifmeelbeskikbaarheid en kiemkrag val saam met meeste besoeke deur *P. cafer*, en lei tot 'n betreklike hoë graad van saadvorming. *Nectarinia violacea* (Jangroentjie) besoek *M. hirtus* af en toe maar dra nie veel stuifmeel oor nie.

Introduction

Proteaceae constitute one of the major components of fynbos vegetation in the south-western Cape region of South Africa (Taylor, 1978). *Protea* is the only genus within this group whose pollination biology has been studied intensively (Rourke and Wiens, 1977; Wiens, Rourke, Casper, Rickart, La Pine and Peterson, 1982). Rodents are the pollinators for many dwarf species, although birds such as the Cape Sugarbird (*Promerops cafer*) and a variety of sunbirds appear to be the major pollen vectors in tall, shrubby

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species (Broekhuysen, 1959; Skead, 1967; Mostert, Siegfried and Louw, 1980).

Another genus of the Proteaceae that is endemic to the southern and south-western Cape, is *Mimetes*. This comprises twelve species, and occurs sporadically from Clanwilliam through the Cape Peninsula and Hottentots Holland Mountains, to Formosa Peak in the east (Rourke, 1982). One of the most geographically restricted species in this group is *Mimetes hirtus*, occurring in isolated populations on the Cape Peninsula, and on the south coast near Betty's Bay, Hangklip and Hermanus (Rourke, 1982).

Apart from the general observation that *M. hirtus* inflorescences are visited frequently by *P. cafer* and sunbirds, virtually nothing is known of the pollination biology of this species (Vogel, 1954). The main objectives of the present paper, therefore, are to establish whether *P. cafer* and/or sunbirds are significant vectors for *M. hirtus* pollen and whether the selection of inflorescences visited is related to the availability of nectar and viable pollen.

MATERIAL AND METHODS

Study areas

Field investigations were conducted at Betty's Bay, 90 km east of Cape Town on the south coast, and at Kirstenbosch National Botanic Gardens in Cape Town, during July and August, 1982. Topography, soil structure and general vegetation for both of these areas have been described previously (Fagan, 1973; Boucher, 1978).

The study area at Betty's Bay comprised several stands of *Mimetes hirtus* (Proteaceae) and *Erica perspicua* (Ericaceae), in which *Promerops cafer* and Orange-breasted Sunbirds (*Nectarinia violacea*) were the dominant nectarivores. Male and female *P. cafer* actively defended non-breeding territories in *M. hirtus* against conspecific birds and *N. violacea. N. violacea* was more frequently seen amongst *E. perspicua* than *M. hirtus*. The area in which plant and bird observations were made was located on a narrow belt of coastal seepage fynbos at the southern foot of Elephant Rock Mountain (Boucher, 1978).

Studies at Kirstenbosch were conducted using a group of 13 *M. hirtus* that had been grown from cuttings planted in poorly-drained soil on the lower south-eastern slopes of Table Mountain. No nectarivores were seen visiting inflorescences during the study period, possibly because of the small *M. hirtus* population, and the availability of numerous alternative nectar sources. Nevertheless, this site proved ideal for extended studies of flowering phenology and diurnal variation in nectar availability.

The Plant

M. hirtus is a relatively dense shrub, approximately 1,5 m in height, that bears numerous terminal flowering heads. Individual heads comprise several red and yellow inflorescences (capitula), each of which consists of 8–11 florets surrounded by involucral bracts. As each floret develops, a bent red style emerges from between the bracts, ultimately becoming fully erect when the pollen presenter dehisces from the anthers (Figure 1). Four tiny nectaries (hypogynous scales) are located at the base of each inflorescence, approximately 57 mm from the distal ends of the fully extended styles (Rourke, 1982; Collins, unpublished data).

In the present study, inflorescences in which only some of the styles were fully extended have been categorised as being "partially-open". Inflorescences with all styles erect, but not yet withered, have been classified as "fully-open". At Betty's Bay and Kirstenbosch, the numbers of partially- and fully-opened inflorescences were counted on randomly-selected flowering heads of *M. hirtus* during the study period.

The Birds

Male *P. cafer* weighed 38,2 ± 3,1 g, and had bill lengths of 29,1 ± 1,0 mm (N = 6), whereas corresponding values for *N. violacea* were 9,9 ± 0,6 g and 21,8 ± 0,9 mm (N = 6), respectively. Female birds were slightly smaller than males (Collins, unpublished data).

Patterns of floret opening

At Kirstenbosch, 12 marked inflorescences were observed over a period of eight days. During this time, florets with erect styles were counted at 07h30, 10h30, 13h30 and 16h30. Emergent styles were marked with a coloured felt pen to facilitate counting and subsequent identification. Data gathered were used to estimate diurnal changes in rates at which florets opened, and the time which elapsed between emergence of the first and last florets on each inflorescence.

Retention of pollen on pollen presenters

Pollen smears were taken from pollen presenters at known times after anthesis during experiments at Kirstenbosch. The technique used entailed rubbing a small cube of agar, impregnated with basic fuchsin, against all sides of each pollen presenter. Permanent mounts of cubes were examined microscopically, and the numbers of stained pollen grains counted in four randomly chosen 320 × fields of view (Collins and Briffa, 1982). The presence of pollen was categorised as: +++ (> 60 pollen grains per 320 × field

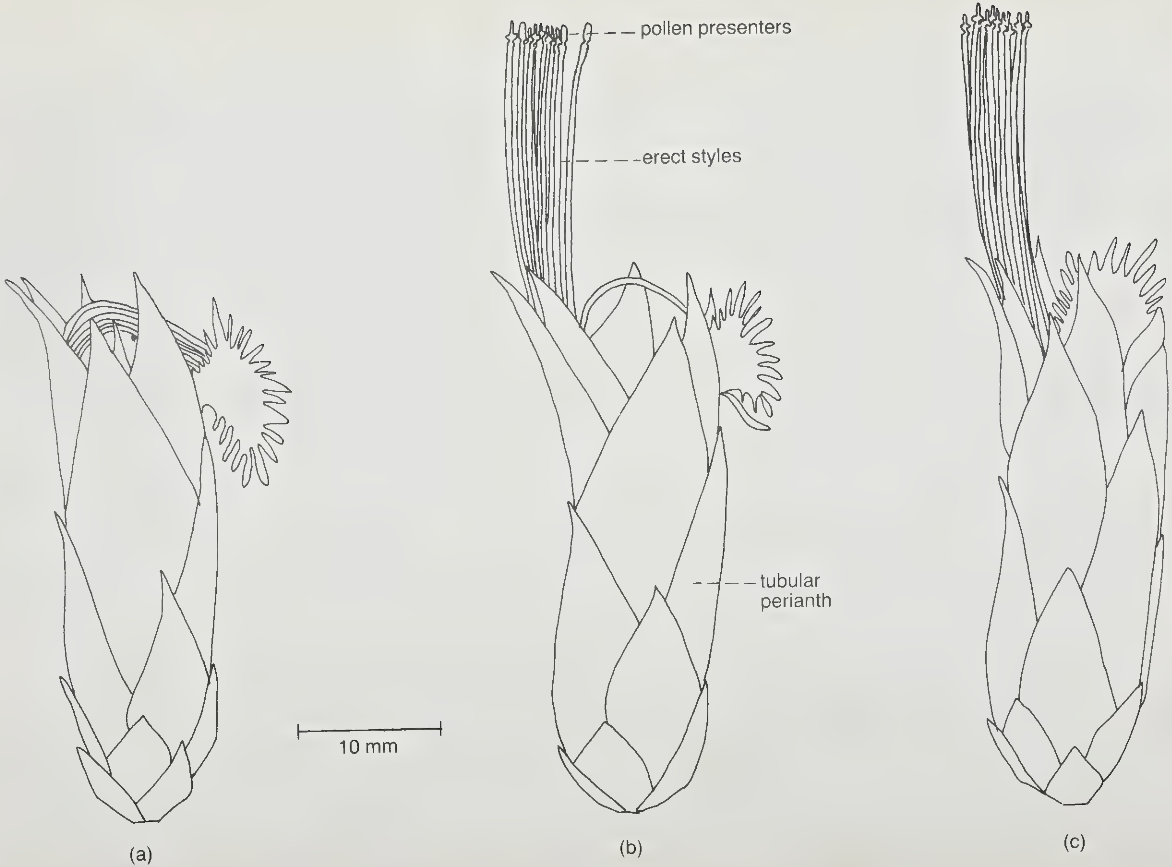

Fig. 1.

Inflorescence of *Mimetes hirtus*, showing florets at various stages of development; (a) unopened, (b) partially-opened, (c) fully-opened.

of view); ++ (10–60 grains per field); + (1–9 grains per field); and 0 (no pollen grains visible).

Additional evidence regarding temporal changes in pollen abundance on pollen presenters of *M. hirtus* was obtained by taking photo-micrographs of fresh terminal portions of styles at 0 and 2 days after anthesis, using a Leitz Laborlux II compound microscope and Wild Photoautomat MPS 45 unit.

Pollen viability

Several styles were collected immediately following anthesis and stored in clean, dry, sealed glass vials. Three pollen samples taken from these styles were smeared onto sterile 1,5 % tap water nutrient agar (Oxoid CM3) at 0, 2 and 5 days after collection. Each smear was examined daily for 5 days, and the percentage germination of pollen grains determined (Stanley and Linskens, 1974). Pollen viability was also tested for at 0 and 7 days by placing samples in drops of 4 % sulphuric acid and looking for signs of "germination" (Stanley and Linskens, 1974).

Nectar availability

Nectar standing crop volumes and percentage equivalent sucrose concentrations (w/w) were measured for individual inflorescences at 07h30, 10h30, 16h30 and 13h30 or 21h30 on two days at Betty's Bay, and four days at Kirstenbosch. On most occasions, five closed, five partially-opened and 10 fully-opened inflorescences were sampled. Volumes were measured using Drummond calibrated capillary tubes, and concentrations with a National temperature-compensated refractometer (Collins and Briffa, 1982; 1983).

Nectarivore foraging behaviour

At Betty's Bay, the manner in which *P. cafer* and *N. violacea* probed *M. hirtus* inflorescences was recorded at various times of day. Where possible, it was also noted whether the inflorescences visited were closed, partially-open or fully-open. No observations of this kind were possible at Kirstenbosch.

Pollen transfer by nectarivores

The relative importance of *P. cafer* and *N. violacea* as vectors of *M. hirtus* pollen, and the manner in which pollen transfer was effected, were assessed by examining smears taken from the foreheads, beaks and throats of birds caught in mist nets at Betty's Bay. Smears were prepared in essentially the same way as described earlier, and pollen grains counted after identification by comparison with those in smears taken from known plants (Collins and Briffa, 1982).

Effectiveness of pollination and seed set

Ten flowering heads of *M. hirtus* at Betty's Bay were enclosed with 10 mm mesh chicken wire to exclude *P. cafer* and *N. violacea*. Selection of flowering heads was such that none bore partially- or fully-opened inflorescences at the time of enclosure (August). In November, these heads were examined for evidence of seed set, as were another 10 heads that had not been screened from nectarivorous birds.

RESULTS

Floret opening

Rates at which florets on marked *Mimetes hirtus* inflorescences at Kirstenbosch produced erect styles are outlined in Table 1. There was a consistent trend over four days for highest rates to occur between 10h30 and 13h30, and lowest during the "overnight" period (Kendall's W = 0,78, χ^2 = 9,30, P < 0,01). Only 12 of the marked inflorescences changed from being unopen to completely open during the study period. Of these, two opened in one to two days, two took almost eight days, and the remainder opened at fairly regular intervals between these times ($\bar{x} \pm$ SD = 4,3 ± 2,1 days).

TABLE 1.
Opening of *M. hirtus* florets on marked inflorescences at Kirstenbosch.

Date and parameter	Time of day			
	16h30–07h30 ("overnight")	07h30–10h30	10h30–13h30	13h30–16h30
9–10 August				
Inflor.	20	16	17	17
Florets opening	27	7	16	5
Florets per inflor. h	0,09	0,15	0,31	0,10
10–11 August				
Inflor.	17	15	17	17
Florets opening	7	0	15	7
Florets per inflor. h	0,03	0,00	0,29	0,14
11–12 August				
Inflor.	16	16	16	15
Florets opening	14	4	21	6
Florets per inflor. h	0,06	0,08	0,44	0,13
12–13 August				
Inflor.	13	13	13	11
Florets opening	0	8	15	1
Florets per inflor. h	0,00	0,21	0,38	0,03

The numbers of fully- and partially-opened inflorescences on 12 marked *M. hirtus* flowering heads at Kirstenbosch varied slightly during the study period, although values of 3,4 ± 2,3 and 1,7 ± 1,2 inflorescences per head respectively, on 9th August give a typical indication of relative abundance. Corresponding values for 39 marked flowering heads at Betty's Bay on 25th July were 4,5 ± 3,5 and 1,2 ± 1,7 inflorescences per head. Comparisons of equivalent values for the two sites show no significant differences, although there were always more fully- than partially-opened inflorescences present (Kirstenbosch: $t = 2{,}27$, $P < 0{,}05$; Betty's Bay: $t=5{,}30$, $P < 0{,}001$).

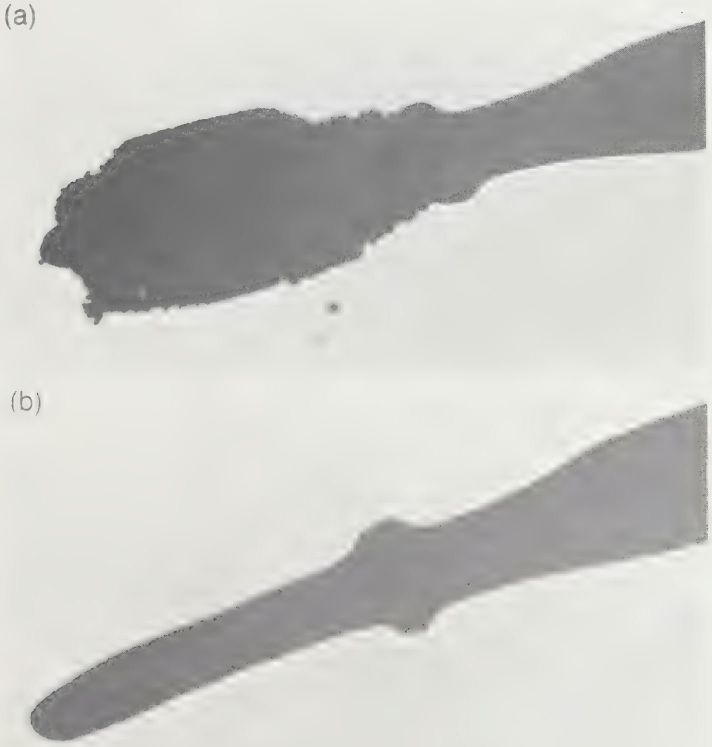

FIG. 2.
Terminal portions of *Mimetes hirtus* styles, showing pollen on pollen presenters (a) at time of anthesis, and (b) 2 days later. Magnification is 40× natural size.

Retention of pollen on florets

Pollen is extremely abundant on freshly exposed pollen presenters of *M. hirtus* (Figure 2, Table 2). Exposure for 15 to 18 hours, however, reduced abundance significantly. After two to three days, there was virtually no pollen left on presenters at Kirstenbosch.

Pollen viability

Germination of freshly-released pollen on nutrient agar was approximately 30 % successful (Table 3). However, viability of pollen decreased significantly with age, with five-day-old pollen exhibiting only 3 % germination.

TABLE 2.
Presence of pollen grains in smears taken from pollen presenters of *M. hirtus*.

Time after exposure of pollen presenter (h)				
0	0–3	3–6	15–18	>192
+++	+++	+++	++	+
+++	+++	+++	++	+
+++	+++	+++	++	+
+++	++	++	+	+
+++	++	++	+	0
+++	++	++	+	0
+++	++	++	+	0
+++	++	++	+	0

Five 320 × microscopic fields of view were examined on each of 40 smears; +++ denotes an average of >60 pollen grains per field of a particular smear; ++ 10–60 grains per field; + 1–9 grains per field; 0 no grains visible.

TABLE 3.
Germination of *M. hirtus* pollen grains at intervals following exposure on pollen presenters.

Date trial initiated	% germination on day 1	% germination on day 3	% germination on day 6
17 August	0,0 ± 0,0 (300)	33,3 ± 2,7 (186)	28,9 ± 3,8 (187)
19 August	0,0 ± 0,0 (300)	16,7 ± 10,9 (180)	......
22 August	0,0 ± 0,0 (300)	3,2 ± 2,1 (181)	......

Numbers in parentheses denote total pollen grains counted on each occasion (not all grains on agar plates counted).

A similar pattern was shown by data generated when fresh or seven-day-old pollen was placed in 4 % sulphuric acid. "Germination" was 84,7 ± 3,6 % successful in the first instance, and 4,8 ± 4,3 % in the latter (at least 200 pollen grains counted in each of the three samples for both treatments; t = 24,68; P < 0,001).

Nectar availability

Nectar standing crop volumes for partially- and fully-opened *M. hirtus* inflorescences at Betty's Bay are shown in Table 4. Values do not vary significantly from one time of day to another or between fully- and partially-opened inflorescences, except for volumes at 07h30 in partially-opened inflorescences, which are significantly greater than most other values (P < 0,01 for 5 out 7 possible comparisons on 28th August).

At Kirstenbosch, standing crop volumes for unopened, partially- and fully-opened inflorescences were much greater than those at Betty's Bay, and showed no significant diurnal variations (Figure 3). Volumes were generally similar for the same types of inflorescences, at the same times of day, despite changes in air temperature and incidence of rain. Nevertheless, there was a consistent trend for smaller volumes to occur in fully- rather than partially-opened inflorescences (Mann-Whitney U > 42, P < 0,05, in 9 out of 14 possible comparisons; t > 2,36, P < 0,05, in 12 of the same comparisons). Volumes in unopened inflorescences were variable, usually being very small except in instances where the inflorescences opened readily when touched.

TABLE 4.
Nectar standing crop volumes ($\mu\ell$) for *M. hirtus* at Betty's Bay.

Date and condition of inflor.		Time of day				
		07h30	10h30	13h30	16h30	21h30
26 July	(a)	......	......	......	......	......
	(b)	3,3 ± 8,4	0.8 ± 1,3	......	4,1 ± 12,6	4,1 ± 7,6
28 Aug.	(a)	22,6 ± 21,9	3,8 ± 3,4	0,9 ± 1,0	2,1 ± 2,2	......
	(b)	2,8 ± 5,3	4,1 ± 9,1	1,6 ± 2,6	0,8 ± 2,0	......

Sample size was 12 in every instance; (a) and (b) denote partially- and fully-opened inflorescences, respectively.

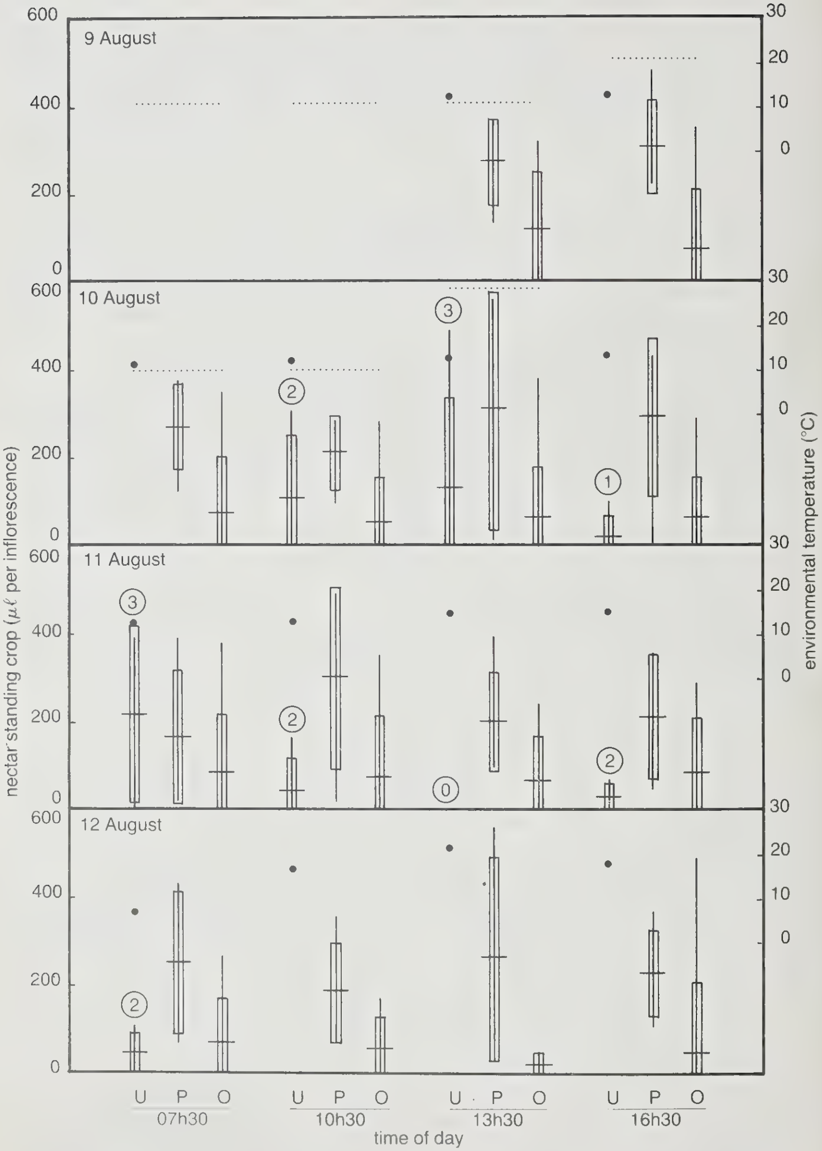
9 August
10 August
11 August
12 August
600
400
200
0
30
20
10
0
nectar standing crop (μℓ per inflorescence)
environmental temperature (°C)
③
②
①
⓪
U P O
07h30
10h30
13h30
16h30
time of day

FIG. 3.

Additional measurements at Kirstenbosch showed that standing crop volumes varied according to the number of erect styles in partially-opened inflorescences (323,1 ± 172,1 $\mu\ell$ when one to two styles erect, 183,6 ± 93,4 $\mu\ell$ when seven or more styles erect; N = 10 in each instance; t = 2,25; P < 0,05). Data used for this comparison were collected at 10h30, three days after the main experimental period, although overall volumes for the 20 inflorescences (253,4 ± 152,6 $\mu\ell$) did not differ significantly from those indicated in Figure 3.

Few nectar concentrations were measured at Betty's Bay, but the values obtained (16,1 ± 1,6%, N = 5) were similar to those for Kirstenbosch (Table 5). There was a tendency for nectar concentrations at Kirstenbosch to be slightly greater for fully- than partially-opened inflorescences, although differences were not statistically significant.

Bird foraging behaviour

Without exception, *Promerops cafer* foraged on *M. hirtus* inflorescences at Betty's Bay while perching on top of the flowering heads (150 observations). Consequently, the birds had to reach over the distal ends of any erect styles in order to probe the inflorescences, thereby brushing their throats against the stigmas and pollen presenters. Fewer *Nectarinia violacea* were seen foraging on *M. hirtus* (20 observations), although all of these consistently perched to the side of, or beneath, the inflorescences that they probed. As a consequence, *N. violacea* rarely brushed against the stigmas or pollen presenters of erect styles.

It was not possible to watch individual *N. violacea* for long enough at Betty's Bay to ascertain whether they preferred *M. hirtus* inflorescences at particular stages of development. However, a territorial female *P. cafer* that could be watched for most of the day showed a clear preference for partially-opened inflorescences (unopened: 107 probes; partially-opened: 704 probes; fully-opened: 113 probes). It is not known whether this pattern is typical of *P. cafer*, in general. Nevertheless, the observed total numbers of inflorescences probed per flowering head by several *P. cafer* and *N. violacea* were significantly greater than the numbers of partially-opened inflores-

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FIG. 3.

Nectar standing crop volumes for *Mimetes hirtus* inflorescences at Kirstenbosch. Vertical lines indicate ranges of values, horizontal lines means, and rectangles one standard deviation either side of the means. The letters U (sample size 5), P (sample size 5) and 0 (sample size 10) represent data for unopened, partially- and fully-opened inflorescences, respectively. Figures enclosed in circles denote the numbers of closed inflorescences that opened partly when touched. Symbols ● and · · · denote air temperatures and occurrence of rain, respectively, at various times of day.

Table 5.
Nectar concentrations (% w/w) for *M. hirtus* at Kirstenbosch.

Date and condition of inflor.		Time of day			
		07h30	10h30	13h30	16h30
9 Aug.	(a)	......	......	17,7 ± 2,2 (6)	17,4 ± 0,6 (5)
	(b)	......	......	16,7 ± 3,1 (5)	21,0 ± 4,3 (5)
10 Aug.	(a)	16,7 ± 2,8 (5)	16,5 ± 1,9 (5)	14,6 ± 1,2 (4)	16,5 ± 2,5 (4)
	(b)	18,8 ± 2,6 (7)	16,6 ± 1,9 (3)	15,8 ± 1,0 (4)	14,8 ± 4,5 (5)
11 Aug.	(a)	13,5 ± 1,2 (5)	15,7 ± 1,1 (5)	15,5 ± 1,8 (5)	14,5 ± 0,9 (5)
	(b)	18,0 ± 5,9 (6)	16,0 ± 1,7 (5)	16,2 ± 2,1 (3)	16,5 ± 2,4 (4)
12 Aug.	(a)	16,0 ± 1,3 (5)	15,4 ± 1,2 (5)	15,4 ± 0,7 (5)	14,4 ± 0,7 (5)
	(b)	16,8 ± 1,2 (5)	19,6 ± 3,8 (4)	20,3 ± 5,5 (2)	18,8 (1)

(a) and (b) have same meanings as in Table 4. Sample sizes given in parentheses.

Table 6.
Comparison of observed abundances of inflorescences and nectarivore probing on flowering heads of *M. hirtus*.

	Partially-opened inflor. per head	Fully-opened inflor. per head	Inflor. probed per head by ♂ *P. cafer*	Inflor. probed per head by ♀ *N. violacea*
$\bar{x}$	1,2	4,5	3,6	3,0
SD	1,7	3,5	2,4	3,0
Range	0–7	0–14	1–11	1–5
N	39	39	67	28

TABLE 7.
Pollen carried by nectarivores at Betty's Bay.

Birds species	Sex and sample size	Pollen present on birds					
		Head			Throat		
		M. hirtus	Erica sp.	Other	M. hirtus	Erica sp.	Other
Promerops cafer	5 ♂	61,2 ± 87,7	0,0 ± 0,0	0,2 ± 0,5	44,0 ± 20,2	0,0 ± 0,0	0,4 ± 0,6
	3 ♀	94,0 ± 85,0	0,0 ± 0,0	1,7 ± 1,5	97,7 ± 38,6	0,0 ± 0,0	0,0 ± 0,0
Nectarinia violacea	7 ♂	1,7 ± 1,1	1,1 ± 1,2	0,3 ± 0,5	3,0 ± 2,4	0,7 ± 1,0	0,0 ± 0,0
	1 ♀	1,0	5,0	0,0	2,0	13,0	0,0

cences available per head at any given time (Table 6; *P. cafer*: t = 5,49, P < 0,001; *N. violacea*: t = 3,12, P < 0,01)

Pollen transfer

The majority of pollen grains collected from *P. cafer* and *N. violacea* at Betty's Bay were derived from *M. hirtus* (Table 7). Variability of pollen grain counts in different smears was considerable, although it is obvious that *N. violacea* carried significantly less pollen than *P. cafer*. Similar pollen loads were borne by head and throat regions, regardless of the nectarivore species involved.

Effective seed set

Seed set in 10 *M. hirtus* flowering heads to which nectarivores had access at Betty's Bay was relatively high, and significantly greater than in 10 heads enclosed by wire mesh (Table 8).

TABLE 8.
Seed set in *M. hirtus* at Betty's Bay.

Parameter	Exposed flowering heads	Enclosed flowering heads
Total inflorescences studied	107	121
Total inflorescences containing seed	38	1
% seed set	35,5	0,8

DISCUSSION

There has been a resurgence of interest in the pollination biology of plants in recent years (e.g. Faegri and van der Pijl, 1971; Heinrich, 1975; Wolf, 1975; Rourke and Wiens, 1977; Carpenter, 1978; Armstrong, 1979; Ford, Paton and Forde, 1979; Hopper, 1980; Frost and Frost, 1981; Collins and Briffa, 1982; Collins and Briffa, 1983). Much has been written regarding pollination and utilization of floral nectar by mammals, birds and invertebrates, although attention has also been paid to the significance of pollen transfer in terms of gene flow and plant population structure (e.g. Beattie, 1978; Levin, 1978).

Despite the general interest shown in pollination in other parts of the world, relatively little attention has been paid to this aspect of plant biology in southern Africa. Virtually the only major studies in this area have concerned the pollination of various *Protea* species (Rourke and Wiens, 1977;

Wiens *et al.*, 1982), and *Strelitzia nicolai* (Frost and Frost, 1981). In the latter case, a variety of sunbirds (Nectarinidae) appear to be the major pollen vectors and users of floral nectar. Some *Protea* species are also pollinated by sunbirds and Cape Sugarbirds, although rodents appear to transfer pollen in many instances. Invertebrates do not seem to play a vital role for any of these plants, although they may do so in other groups.

It has been suggested that members of the Proteaceae such as *Mimetes* are pollinated primarily by birds (Skead, 1967; Rourke, 1982). Qualitative data have not been published previously in support of this contention, although it is obvious that inflorescences of members of this genus have many features that are allegedly characteristic of bird-pollinated plants: bright colouration, ease of access from above, diurnal availability of nectar and tubular perianths (Faegri and van der Pijl, 1971; Carpenter, 1978; Hopper, 1980). Direct observations made in the present study, however, confirm that, at least at Betty's Bay, *Promerops cafer* and *Nectarinia violacea* are frequent visitors to *Mimetes hirtus*. Intermittent observations of inflorescences during the day and at night failed to detect any mammalian visitors. The only invertebrates present were small Hemiptera (2,7 ± 2,5 per inflorescence, N = 10), and these appeared to be confined to perianth tubes, rarely moving on to the styles (Collins, unpublished data).

Evidence obtained at Betty's Bay during the present study demonstrates that *P. cafer* is a major pollen vector for *M. hirtus*, although *N. violacea* appears to be much less important. This difference could be a function of the strongly territorial behaviour of *P. cafer*, which allows *N. violacea* relatively few opportunities to probe inflorescences. It is likely, however, that differences in foraging behaviour are more important. As the subordinate nectarivore, *N. violacea* is probably forced to rely on fully-opened inflorescences, with their relatively low nectar rewards. Consequently it would only rub its head and throat against dehisced anthers. The existence of substantial pollen loads on both throats and heads of *P. cafer* is consistent with the foraging behaviour of this species, particularly as its preference is for partially-opened inflorescences in which it could presumably induce anthesis as its head brushed against unopened florets. The significance, if any, of higher rates of floret opening between 10h30 and 13h30 is not apparent.

M. hirtus is protandrous, with pollen exposure on a given floret occurring before the stigmatal groove is receptive (Rourke, personal communication). Effective transfer of pollen between one floret and another is therefore dependent upon vectors such as *P. cafer* brushing against pollen presenters and stigmata at appropriate stages in their development. Pollen availability on individual presenters decreases significantly within 15 h of anthesis, even at sites such as Kirstenbosch where nectarivores rarely visit *M. hirtus*. However, it takes several days for all florets on an inflorescence to open, thereby extending the duration of pollen-availability on the inflorescence. Nevertheless, viability of any pollen that remains on pollen presenters is reduced significantly after two days. It is obvious, therefore, that effective outcrossing is unlikely unless vectors visit inflorescences that are partially- or just completely-opened. In this context, it would seem significant that *P. cafer* has a definite preference for partially-opened inflorescences, although it sometimes probes others. It is not known when the stigmatal grooves of *M. hirtus* are receptive, although this would most appropriately occur when birds are visiting inflorescences on which most of the florets were open.

Partially-opened *M. hirtus* inflorescences at Kirstenbosch produce standing crop volumes of relatively dilute nectar that are larger than most values reported for other plants (e.g. Ford, 1979; Frost and Frost, 1981; Collins and Briffa, 1982; 1983). There is no significant variation from one time of day to another, possibly because nectarivores rarely visit the inflorescences. With few exceptions, unopened and fully-opened inflorescences contain little nectar. These observations suggest that nectar production by *M. hirtus* varies according to the age of the inflorescences, a trend similar to that reported for several other plant species (e.g. Frost and Frost, 1981). Standing crops at Betty's Bay are much smaller than at Kirstenbosch, possibly because of differences in soil water potential (Fagan, 1973; Boucher, 1978) and greater nectar demand by *P. cafer* and *N. violacea*. At this site, nectarivore pressure during the day is almost certainly responsible for the lack of significant differences between standing crops for partially- and fully-opened inflorescences at all times except shortly after dawn (07h30). This explanation is consistent with the observed foraging preference of *P. cafer* for partially-opened inflorescences.

The *M. hirtus–P. cafer* system is clearly well adapted for pollen transfer. Nectar rewards are greatest in inflorescences that are releasing pollen, thereby attracting *P. cafer* at a time when maximum pollen transfer can occur. The effectiveness of this system is demonstrated by the relatively high level of seed set that results from exposure of *M. hirtus* to *P. cafer* (and *N. violacea*). Restriction of *M. hirtus* to small isolated populations in the southwest Cape would not seem to be caused by any deficiencies in this system, but rather because of the need for habitats containing acidic, peaty soils (Rourke, personal communication) and/or the territorial nature of the major pollinator, *P. cafer*.

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